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CLASSIFICATION OF THE OVIPENNIS AND TRIFARIA GROUPS OF *NEBRIA* LATREILLE (COLEOPTERA: CARABIDAE: NEBRIINI)

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This study of western high altitude *Nebria* began with our discovery of a new form on Circleville Mountain in southern Utah. This new form is related to *Nebria trifaria* LeConte, and because we are opposed in principle to publication of isolated descriptions of new taxa (Ball and Erwin, 1969), we surveyed the trifaria group of species in seeking more information about the relationships of this new form. In turn, this led us to reexamine Lindroth's (1961) study of North American *Nebria*, which further led us to examine other *Nebria* species groups occurring in the mountains of western United States. Our data on two of these groups are presented here.

On the basis of more extensive material than was available to Lindroth, we have slightly rearranged his groups; revised part of his key to accommodate our new forms; and we have provided illustrations of diagnostic characteristics not illustrated by him.

MATERIAL

We examined 719 adult specimens of the ovipennis and trifaria groups. The number of specimens of each taxon is given with the respective descriptions. We have also seen numerous additional specimens of *Nebria* representing species not reported on here, which helped in our understanding of the genus in North America.

The following letter code denotes museums or private collections whose material we examined: CAS—California Academy of Sciences,

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San Francisco, California 94118; DHKa—David H. Kavanaugh, GRNo—Gerald R. Noonan, and UASM—Strickland Museum, Department of Entomology, University of Alberta, Edmonton 7, Alberta, Canada; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; OUCO—Ohio State University, Columbus, Ohio 43210; SJSC—San Jose State College, San Jose, California 95114; TLEr—personal collection of senior author; UCD—University of California, Davis, California 95616; UCR—University of California, Riverside, California 92502.

METHODS

These have been described in detail previously (Ball and Erwin, 1969; Erwin, 1970).

We define subspecies as geographically (or temporally) isolated populations within a species that differ taxonomically from other such populations (but which are potentially capable of interbreeding with these other subspecies). The evidence for meeting the criteria is derived from morphological and distributional data, only.

An exclamation point (!) is used here to indicate type-specimens seen by us.

The only measurement presented is total length. This was made with an ocular micrometer in a Wild binocular microscope. At the magnification used, one unit equalled 0.07 mm.

NOTES ABOUT THE STRUCTURE OF THE FEMALE REPRODUCTIVE SYSTEM

Females for study should be killed and preserved in a histological fixative, such as Bouin's solution. Our observations, however, were of museum specimens known to have been killed in cyanide or ethyl acetate fumes. Thus, the observations are tentative and must be confirmed with material especially prepared for study of lightly sclerotized tissue.

The bursa copulatrix of a nebriine female (Fig. 36) is a large, saclike structure diverted anterodorsally from the common oviduct. This sac has a characteristic shape which differs from species group to species group.

Among females of the trifaria and ovipennis groups and *N. paradisi* Darlington, the spermathecal duct arises from the dorsal surface of the bursa (Fig. 36), and extends to the lanceolate-shaped spermathecal reservoir. Near the origin of the duct, the membrane of the bursa is various, differing among groups of species, interspecifically and intraspecifically. In females of *N. hudsonica,* the bursal sclerite and spermatheca are located ventrally.

Females of *N. purpurata* and *N. trifaria* exhibit a sclerite on the dorsal surface of the bursa, near the point of origin of the spermatheca. This sclerite varies in form both among and within population samples of *N. trifaria*, but the intrapopulation variation is slight compared to the amount of interpopulation difference.

TAXONOMY

Nebria Latreille

Nebria Latreille, 1802: 89. Type-species.—*Carabus brevicollis* Fabricius, 1792: 150. (See Lindroth, 1961: 60 for nomenclatorial remarks about the type species.)

Diagnostic characteristics: Head with one supraorbital seta over each eye; scrobe of mandible unisetose; stipes and mentum without spiniform setae; mentum with tooth broadly truncate or bifid; anterior coxae uniperforate-separate, open behind; anterior tibia anisochaetous-sulcate; middle coxae disjunct-confluent; hind coxae conjunct-confluent, lateral margin or "wing" vertical; elytra each with short scutellar stria and nine complete striae; male genitalia with unarmed internal sac (sac shape various) and glabrous unequal parameres; styli of ovipositor each with bisetigerous ventral puncture; bursa copulatrix various (Figs. 36–41); proventriculus internally with four large, coarse teeth (Fig. 22), each with two external projections alternated with four rows of dense brushes; (Figs. 21, 22); proventricular teeth of two types, one with broad smooth concavity, three more linearly convex, without smooth areas. Size medium to large (length 7.5–17.0 mm, from Lindroth, 1961).

REVISED PORTION OF LINDROTH'S KEY TO THE NORTH AMERICAN SPECIES OF *NEBRIA* (1961).

(to be inserted at couplet number 19, replacing 19–27:
page numbers given below refer to this paper)

19. Pronotum without posterior lateral seta; with deep furrow inside hind angle (Fig. 9) .... *N. kincaidi* Schwarz, p. 85.
Pronotum with lateral setigerous puncture just in front of hind angle .... 20.

20. Hind coxa at base (except in *hudsonica* and, individually in *paradisi*) and sterna III-V plurisetose (not all three sterna in some specimens of *paradisi*) .... 21.
Hind coxa and sterna III-V (except for asymmetrical anomalies) unisetose .... Couplet 36 in Lindroth

21. Humeri narrow, sloped; elytra broadest in apical half, basal setigerous puncture (between striae one and two) absent in most specimens; wings reduced, with or without bare suggestion of reflexed apex .... 22a.
Humeri prominent; elytra rather parallel-sided; basal setigerous puncture present; wings with complete reflexed apex .... Couplet 28 in Lindroth

22a. Abdominal sternum II with setae between hind coxae .... 23a.
Abdominal sternum II without setae between hind coxae .... 24a.

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23a. Tarsal articles short and robust (Fig. 4); scape of antenna swollen, widest about middle .... *N. ovipennis* LeConte, p. 81.

Tarsal articles long and narrow (Fig. 5); scape of antenna narrower, widest apically .... *N. spatulata* Van Dyke, p. 83.

24a. Metasternum subequal to or longer than diameter of middle coxa (Fig. 7). Elytra ellipsiform, widened only slightly from humeri to basal third. Wing rudiment with suggestion of reflexed apex .... 25a.

Metasternum shorter than diameter of middle coxa (Fig. 6). Elytra oviform. Wing rudiment without trace of reflexed apex .... 30a.

25a. Pronotum with sides widely reflexed (Fig. 8); lateral bead effaced at anterior angle. Scape of antenna swollen apically. Head, pronotum and elytra broad .... 26a.

Sides of pronotum not or barely reflexed (Fig. 2); lateral bead clearly engraved at anterior angle (Fig. 2). Antennal scape almost cylindrical. Head, pronotum and elytra narrow .... *N. purpurata* LeConte, p. 89.

26a. Elytron with intervals 3, 5 and 7 strongly catenate. Dorsal surface piceous, not metallic. Median lobe with apical portion as in Figures 26, 28, 29 .... 27a.

Elytral intervals 3, 5 and 7 with few catenations, interval 5 of some males not catenate. Dorsal surface shiny, elytra violaceous metallic. Median lobe with apical portion as in Figure 27; known only from Circleville Mt. of southern Utah .... *N. trifaria piute* new subspecies, p. 95.

27a. Male median lobe with apical portion as in Figure 26; locality, mountains of central Utah, southern Wyoming or eastern Nevada (Fig. 42) .... *N. trifaria trifaria* LeConte, p. 93.

Apex of median lobe and range not as above .... 28a.

28a. Median lobe with apical portion as in Figure 29; locality, Rocky Mountains of southern Colorado and eastern Utah (Fig. 42) .... *N. trifaria catenata* Casey, p. 97.

Apex of median lobe and range not as above .... 29a.

29a. Median lobe with apical portion as in Figure 28; locality, Rocky Mountains of southern Wyoming, northern and central Colorado (Fig. 42) .... *N. trifaria coloradensis* Van Dyke, p. 96.

Median lobe with apical portion as in Figure 25; locality, Grand Teton Mountains, Wyoming (Fig. 42) .... *N. trifaria tetonensis* new subspecies, p. 95.

30a. Mentum with tooth broadly truncate. Tarsus with articles short and robust (Fig. 4), especially in male; (median lobe of *ingens* Horn as in Fig. 33) .... "ingens Group."

Mental tooth bifid. Tarsus with articles long and narrow (Fig. 5) .... 31a.

31a. Elytra piceous to black, each with intervals 3, 5 and 7 catenate. Abdominal sterna III-V with group of setigerous punctures laterally at base .... *N. vandykei* Bänninger, p. 87.
Elytra violaceous, metallic, without catenate intervals. Abdominal sterna without lateral setae; male median lobe as in Figure 35 .... *N. paradisi* Darlington, p. 81.

THE OVIPENNIS GROUP

The diagnostic characteristics of this group are as follows. Elytra with narrow humeri, elytral intervals not or weakly catenate; hind wings extremely reduced; sterna III-V with apical setae only; median lobe of male genitalia with pouch in right side; bursa copulatrix without sclerites.

Originally included in this group by Lindroth (1961) were the three species described below plus *Nebria paradisi* Darlington. The latter species is removed on the grounds that males lack the pouch of the median lobe, and hence there is no evidence that *N. paradisi* is related to the other three species. Its true relationships must await further studies.

Nebria ovipennis LeConte

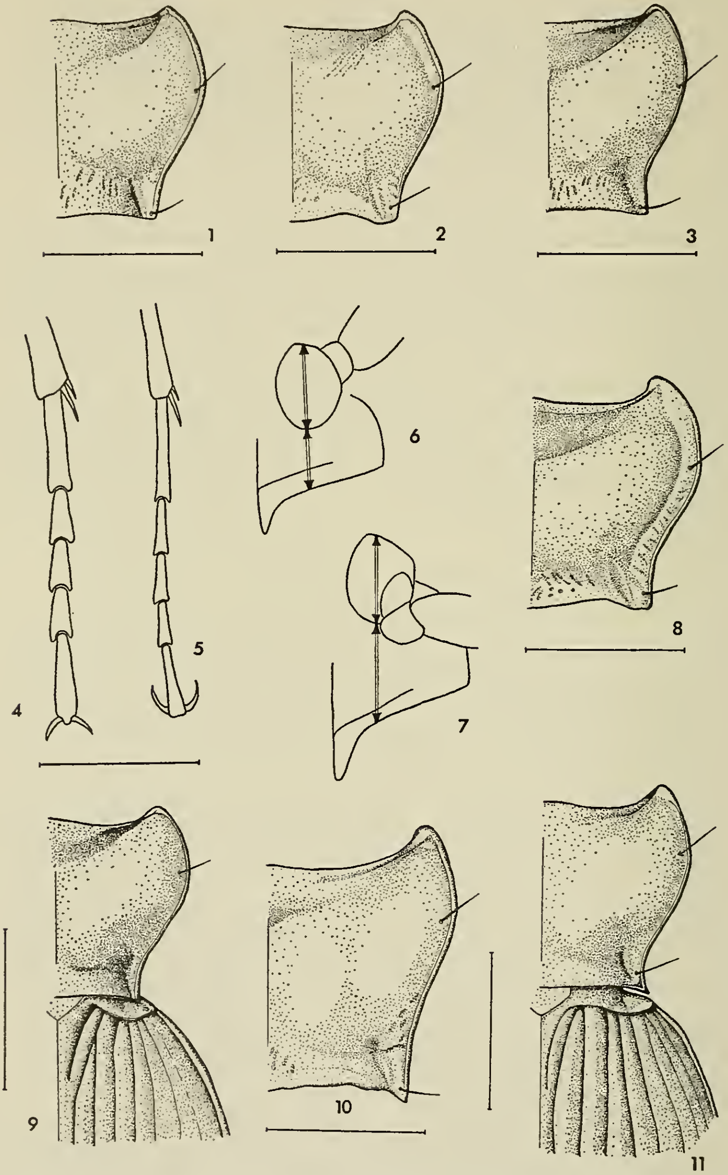
Figures 1, 4, 12, 15, 18, 42

Nebria ovipennis LeConte, 1878: 477. Type-locality.—Sierra Nevada, California, as originally given by LeConte, but here restricted to Chipmunk Flat, Tuolumne County, California, on the basis that the range is restricted to the southern Sierra Nevada. Type a male!, MCZ No. 648.

Diagnostic characteristics: Body dark rufous to piceous, without metallic luster, appendages rufous. Microsculpture of entire dorsal surface isodiametric. Antenna with scape short, robust, widest about middle. Tooth of mentum broadly truncate or bifid. Head and pronotum very broad, pronotum wider than one elytron, sides narrowly reflexed, anterior and posterior angles produced, posterior angles acute. Elytra oviform, interval 7 partially catenate or not. Middle coxa with longitudinal diameter much greater than length of metasternum behind middle coxa. Tarsus with articles short and robust, especially in male (Fig. 4). Male median lobe with long broad pouch on right side (Figs. 15 and 18). Stylus of female ovipositor as in Figure 36. Total length 10.9–12.1 mm. Material dissected: three males, one female.

Geographical distribution: The members of this species are in the Sierra Nevada of California, ranging from Tulare County in the south to at least Placer County in the north (Fig. 42). We have studied 19 specimens from the following localities.

CALIFORNIA: ALPINE COUNTY: Ebbetts Pass 8,730′ 25 June (MCZ); Gin, July (NMNH). PLACER COUNTY: (NMNH). TULARE COUNTY:



Figs. 1–3, 8 and 10. Pronotum, right dorsal aspect. 1. *Nebria ovipennis* LeC., female, Lake Elizabeth, California. 2. *Nebria purpurata* LeC., female, Canyon of the Big Blue, Colorado. 3. *Nebria spatulata*

Franklin Lake, 8 September (MCZ); Mount Silliman, 10,000′, September (CAS). TUOLUMNE COUNTY: Chipmunk Flat, 9 August (UCR); Lake Elizabeth 11,000′, 6 August (CAS); above Lundy, 9,000–11,000′, 9 July (USNM); Sonora Pass, 9,626′, 27 July (GRNo); Tuolumne Meadows, 27 July (CAS, MCZ).

One specimen is labelled Eugene, Oregon (MCZ). We doubt the authenticity of this record.

Nebria spatulata Van Dyke

Figures 3, 5, 13, 16, 19, 42

Nebria spatulata Van Dyke, 1925: 119. Type-locality.—Franklin Lake, California. Type a female!, No. 1625 (CAS).

Diagnostic characteristics: Color of body rufous to dark piceous, appendages rufous. Microsculpture of dorsum well developed, meshes slightly transverse. Dorsal surface shiny. Antenna with scape elongate, narrow, widened apically. Pronotum narrow, as wide as single elytron; sides narrowly reflexed; anterior and posterior angles produced, latter acute. Elytra ellipsiform, humeri more pronounced than in *ovipennis* specimens. Middle coxa with longitudinal diameter subequal to or slightly greater than length of metasternum behind middle coxa (Fig. 6). Median lobe of male as in Figures 16 and 19, pouch narrower than in *ovipennis* males. Ovipositor of female with stylus as in Figure 36. Total length 11.0–12.4 mm. Material dissected: three males, one female.

Geographical distribution: Members of this species are known from the southern part of the Sierra Nevada of California, from Tulare County to Tuolumne County (Fig. 42). We have seen 14 specimens from the following localities.

CALIFORNIA: FRESNO COUNTY: Brewer Lake, 22 September (CAS). MADERA COUNTY: Mount Lyell, 11,000′, 27 August (CAS). TULARE

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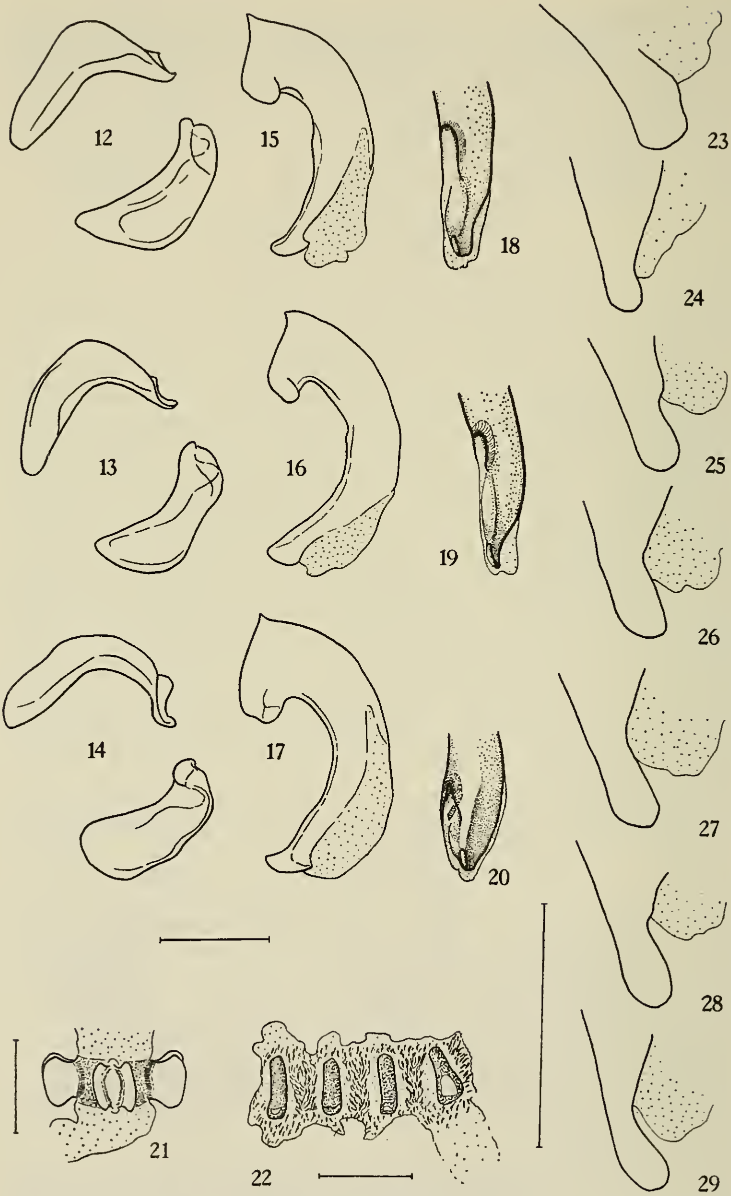
Van Dyke, female, Mt. Lyell, California. 8. *Nebria trifaria tetonensis* n. ssp., female, Cascade Canyon, Wyoming. 10. *Nebria vandykei* Bänninger, female, Mt. Rainier, Washington.

FIGS. 4 and 5. Tarsi of posterior left leg, dorsal aspect, setae not shown. 4. *Nebria ovipennis* LeC., male, Ebbetts Pass, California. 5. *Nebria spatulata* Van Dyke, male, Mt. Lyell, California.

FIGS. 6 and 7. Diagrammatic illustration of metasternum and middle coxa. 6. Metasternum subequal to middle coxa. 7. Metasternum longer than middle coxa.

FIGS. 9 and 11. Pronotum, right dorsal aspect and humeral portion of right elytron. 9. *Nebria kincaidi* Schwarz, male, Seven Lakes Basin, Washington. 11. *Nebria paradisi* Darlington, female, Mt. Rainier, Washington.



FIGS. 12–14. Right and left parameres of male genitalia, ventral aspect. 12. *Nebria ovipennis* LeC. 13. *Nebria spatulata* Van Dyke, Mt. Lyell,

COUNTY: Franklin Lake, 8 September (MCZ); Mount Silliman, 10,000′, 3 August (CAS). TUOLUMNE COUNTY: Chipmunk Flat, 9 August (UCR); Tioga Pass, 10,000′, 24 August (CAS).

Nebria kincaidi Schwarz

Figures 9, 14, 17, 20, 42

Nebria kincaidi Schwarz, 1900: 525. Type-locality.—Farragut Bay, Alaska. Type a male!, No. 56138 (USNM).

Nebria columbiana Casey, 1913: 48. Type-locality.—Inverness, British Columbia. Type a male!, No. 46848 (USNM).—Lindroth, 1961: 88.

Diagnostic characteristics: Color of body dark piceous to black, elytra (also head and pronotum of some specimens) vividly metallic purple with green-coppery luster. Microsculpture of dorsal surface with lines finely impressed, meshes transverse. Antenna with scape moderately robust, slightly swollen toward apex. Head and pronotum narrow, pronotum slightly wider than one elytron, sides moderately reflexed and narrowed behind to slightly acute hind angles, anterior angles produced, surface convex. Elytra oviform, intervals variously catenate, basal margin at humerus strongly sinuate. Middle coxa with longitudinal diameter greater than length of metasternum just behind middle coxa. Male genitalia (Figs. 14, 17, 20) with median lobe with small narrow pouch in right side. Ovipositor with stylus as in Figure 36. Length 11.2–11.5 mm. Material dissected: three males, one female.

Geographical distribution: According to Lindroth (1961), these beetles range from northern Oregon to southern Alaska. See this refer-

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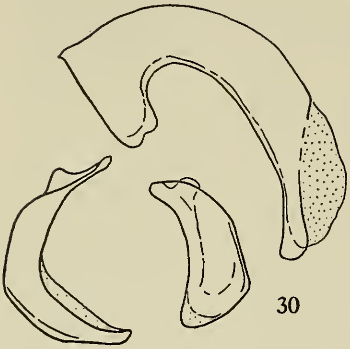
California. 14. *Nebria kincaidi* Schwarz.

FIGS. 15–17. Median lobe of male genitalia, left lateral aspect. 15. *Nebria ovipennis* LeC. 16. *Nebria spatulata* Van Dyke, Mt. Lyell, California. 17. *Nebria kincaidi* Schwarz.

FIGS. 18–20. Median lobe of male genitalia, apex, ventral aspect. 18. *Nebria ovipennis* LeC. 19. *Nebria spatulata* Van Dyke, Mt. Lyell, California. 20. *Nebria kincaidi* Schwarz.

FIGS. 21–22. Proventriculus of *Nebria trifaria piute* n. ssp. 21. Lateral aspect. 22. Internal aspect after dissection.

FIGS. 23–29. Apex of median lobe of male genitalia, right lateral aspect. 23. *Nebria vandykei* Bänninger, Paradise Park, Washington. 24. *Nebria purpurata* LeC., Leavenworth, Colorado. 25. *Nebria trifaria tetonensis* n. ssp., Cascade Canyon, Wyoming. 26. *Nebria t. trifaria* LeC., Alta, Utah. 27. *Nebria trifaria piute* n. ssp., Circleville Mt., Utah. 28. *Nebria trifaria coloradensis* Van Dyke, Broadmoor, Colorado. 29. *Nebria trifaria catenata* Casey, North Creek, Utah.



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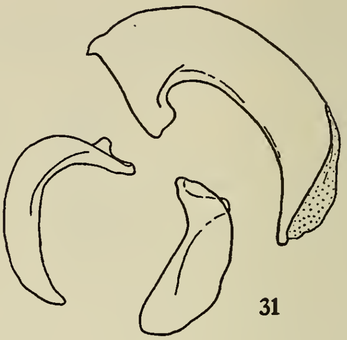

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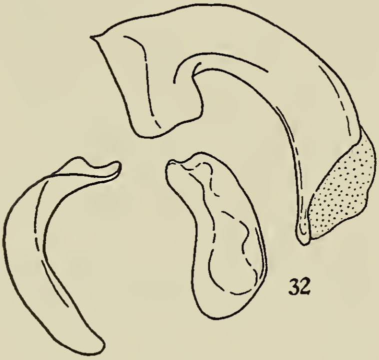

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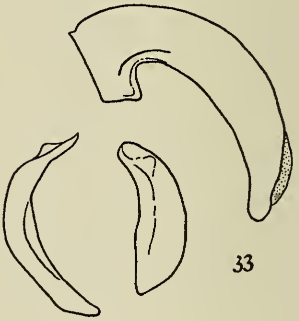

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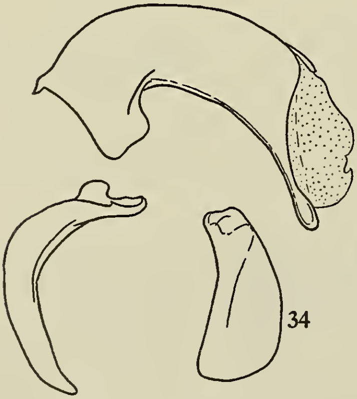

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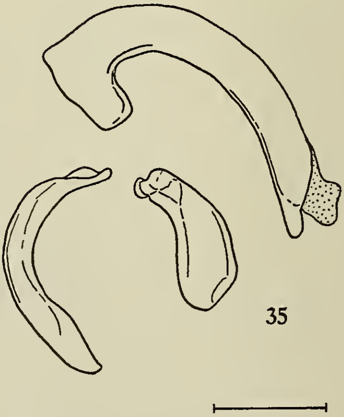

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ence for locality data. We have also seen specimens from the Olympic Peninsula, Washington, and from Mount Rainier.

THE TRIFARIA GROUP

The diagnostic characteristics of this group are as follows. Elytra with narrow humeri, intervals 3 and 7 catenate; hind wings reduced; abdominal sterna III-V each with group of setae laterally at base in addition to two or more apical setae; median lobe of male genitalia with apical portion more or less extended; bursa copulatrix with or without large dorsal median sclerite.

Nebria vandykei Bänninger

Figures 10, 23, 30, 42

Nebria vandykei Bänninger, 1928: 5. Type-locality.—Mount Rainier, Washington. Holotype presumably in Bänninger collection, Zürich.

Diagnostic characteristics: Color of body and appendages dark piceous to black, without metallic luster. Microsculpture of dorsal surface of fine lines, meshes slightly transverse, dorsal surface rather shiny. Scape of antenna swollen, longer than in *trifaria*. Pronotum as in Figure 10, wider than single elytron, sides widely reflexed, anterior and posterior angles very prominent and acute, base coarsely punctate. Elytra ellipsiform, catenations numerous, interval 5 of left elytron of males with five to seven ($N = 7$, mean 5.71), of females with four to six ($N = 11$, mean 5.27). Hind wings without apical reflexed portions, more reduced than those of *trifaria*. Middle coxa with longitudinal diameter about equal to length of metasternum just behind middle coxa. Median lobe of male with apical portion short and very broad (Fig. 23). Female ovipositor with stylus as in Figure 36. Bursa copulatrix without sclerites. Length 13.3–15.5 mm. Material dissected: six males, two females.

Geographical distribution: Members of this species are known from mountains of the Cascades system in Oregon and Washington (Fig. 42). We have seen 26 specimens from the following localities.

OREGON: CLACKAMAS COUNTY: Mount Hood, Sand Creek, 7 July (CAS). WASHINGTON: PIERCE COUNTY: Mount Rainier, 13 July (MCZ, USNM); Paradise Park, 6,000′, Mount Rainier, 15 July (CAS); Paradise River, 5,500′, Mount Rainier, 18 July (CAS).

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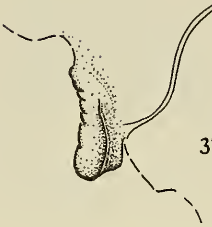
FIGS. 30–35. Male genitalia; parameres, ventral aspect, median lobe, left lateral aspect. 30. *Nebria vandykei* Bänninger. 31. *Nebria purpurata* LeC. 32. *Nebria t. trifaria* LeC. 33. *Nebria ingens* Horn. 34. *Nebria trifaria piute* n. ssp., Circleville Mt., Utah. 35. *Nebria paradisi* Darlington.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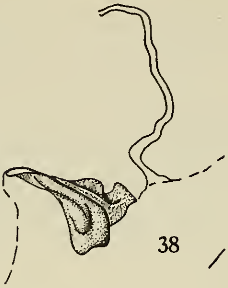
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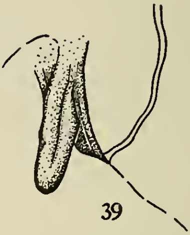
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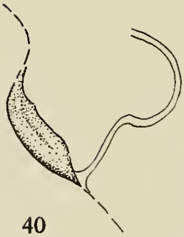
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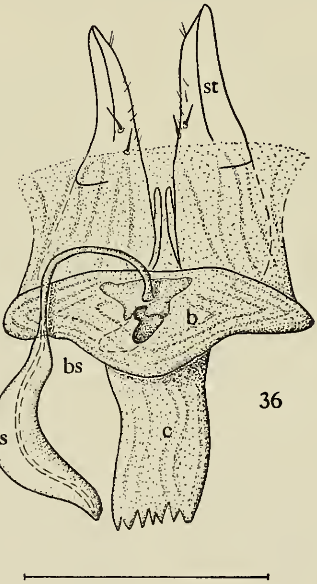

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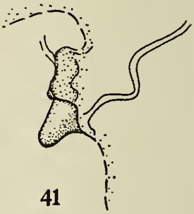
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Fig. 36. Female genitalia of *Nebria trifaria coloradensis* Van Dyke, Longs Peak, Colorado. Symbols: c = common oviduct, b = bursal sac, s = spermathecal reservoir, st = stylus, bs = bursal sclerite.

Figs. 37–41. *Bursal sclerite*, lateral aspect. 37. *Nebria t. trifaria* LeC., Alta, Utah. 38. *Nebria trifaria piute* n. ssp., Circleville Mt., Utah. 39. *Nebria trifaria catenata* Casey, Montrose, Colorado. 40. *Nebria purpurata* LeC., Ouray, Colorado. 41. *Nebria trifaria coloradensis* Van Dyke, Long's Peak, Colorado.

Nebria purpurata LeConte

Figures 2, 24, 31, 40, 42

Nebria purpurata LeConte, 1878: 477. Type-locality.—Leavenworth Valley, Colorado. Type a male!, No. 649, MCZ.
Nebria mobilis Casey, 1913: 50. Type-locality.—Colorado. Type a female! No. 46850, USNM.—Lindroth, 1961: 86.

Diagnostic characteristics: Color of body and appendages excluding elytra, dark piceous to black, elytra vividly metallic purple, blue or green. Microsculpture as in *N. vandykei.* Pronotum as in Figure 2, narrow, sides narrowly reflexed, anterior angles moderately produced, posterior angles about right. Elytra with sides nearly parallel, catenations few, interval 5 of left elytron without or with one to three catenations (males, $N = 25$, mean 0.80; females, $N = 26$, mean 0.50). Length of metasternum as in *N. vandykei.* Median lobe of male as in Figure 31, apical portion very short, width average. Female ovipositor with stylus as in Figure 36. Bursa copulatrix with dorsal sclerite dome-shaped, smooth. Material dissected: five males, two females.

Geographical distribution: Members of this species are known to us from the Rocky Mountains of Colorado; from Rocky Mountain National Park in the north, to Silverton in the south (Figs. 42 and 43). Lindroth (1961: 86) reports specimens from Idaho and Montana, based on literature records, but David H. Kavanaugh informed us that these specimens are members of *N. gebleri* Dejean. We have seen 134 specimens, from the following localities.

COLORADO: BOULDER COUNTY: Ouzel Falls, 24 July (DHKa). CLEAR CREEK COUNTY: Georgetown, 8,300′–8,600′, 15–26 July (MCZ); Leavenworth Valley, above Georgetown, 9,000′–10,000′, June (MCZ, USNM); Silver Plume, 9,000′–10,000′, 15–26 June (MCZ, USNM). GUNNISON COUNTY: Canyon of Big Blue, 8,500′, 5–6 July (MCZ, USNM). LAKE COUNTY: Lake Creek, 7 miles west of Twin Lakes, 16–23 August (DHKa). MINERAL COUNTY: North Creede, 9,500′, 8 July (MCZ); 2 miles west of Wolf Creek Pass, 29 August (DHKa); 4 miles west of South Fork of Rio Grande (DHKa). OURAY COUNTY: Ouray, 9,000′, July (USNM). PARK COUNTY: N. Fork South Platte River, near Hoosier Pass, 11,500′, 12 July (DHKa). PITKIN COUNTY: Lake Creek, 11,200′ (DHKa). SAN JUAN COUNTY: Silverton, 9,800′, June (USNM); valley of Upper San Juan, 7,000′–10,500′, 13–15 August (USNM). SUMMIT COUNTY: Blue Lakes, 10.0 miles south of Breckenridge, 11,483′, 12–19 July (DHKa, TLEr); Monte Cristo Creek, 11,000′, 12 July (DHKa); Quanday Peak, 12,500′, 19 July (DHKa). ROCKY MOUNTAIN NATIONAL PARK: Fall River, 8,600′, 18 August (UASM).

Nebria trifaria LeConte

Nebria trifaria LeConte, 1878: 478. Type-locality.—American Fork Canyon, Utah. Type-specimen a female!, No. 651, MCZ.

Diagnostic characteristics: Color of body and appendages dark piceous to black, not or slightly metallic. Microsculpture of dorsal surface with lines moderately coarse, meshes slightly transverse, elytra slightly dull. Antenna with scape robust, swollen apically, hind edge straight. Pronotum as in Figure 8, wider than elytron, sides widely reflexed, anterior angles strongly produced, base coarsely punctate. Elytra oviform, intervals 3 and 7 variously catenate, interval 5 catenate or not (see below for details). Length of metasternum as in *N. vandykei.* Male genitalia with apical portion of median lobe various, but longer than in *N. purpurata* and narrower than in *N. vandykei* (Figs. 24–29, and see below for details). Stylus of female ovipositor as in Figure 36. Bursa with dorsal sclerite, variously formed (Figs. 37–41, and see below for details.)

Geographical distribution: The range of this species extends from the Grand Teton Mountains of Wyoming southward to southern Colorado, and from the front range of the Rockies to northeastern Nevada. (See Figs. 42 and 43.)

Variation patterns: The following characteristics exhibit geographical variation: color; number of catenations in elytral interval 5; form and proportions of the male median lobe; and form of the bursal sclerite of females. The variation pattern of each characteristic is described below.

Variation in color: The dorsal surface is black in all specimens except those from Circleville Mountain (No. 6). The elytra of the latter specimens are dull purple.

Catenations in elytral interval 5: Data for population samples from 14 areas are provided in Table 1. Each area is numbered, and the position of the area is indicated by the appropriate number in Figure 43. The number of catenations was determined for the left elytron, only. The range is from zero to seven among males and from zero to eight among females. For males, both extremes are exhibited by the Mount Linnaeus sample (No. 14). On average, more northern specimens have higher numbers than have more southern specimens. Thus, northern samples tend to have higher mean values than have the southern samples.

In more detail, highest mean values are exhibited by the Wyoming samples. The lowest mean values are in samples from southwestern Utah, next lowest in samples from southeastern Utah (No. 14), and samples with intermediate mean values are in Colorado and northern Utah. The mean differences are slight among samples from areas other than southwestern Utah, and variation is probably clinal from north to south. The southwestern Utah samples differ markedly from their more northern counterparts (0.9 to 5.1 ♂♂, 2.6 to 5.4 ♀♀), and a step-cline is probably the mode of the variation pattern between the former and latter groups of samples.

Another way to analyze the data is to examine the ratio of means of males and females of each sample (Table 1). The ratios are near unity, except for the Circleville (No. 6) sample, in which the value for the ratio is 0.35, and the Montrose sample (No. 12) in which the value is

TABLE 1. Data on variation among population samples of *Nebria trifaria* in number of catenations of interval 5 of left elytron.

Locality	Map reference number	Males			Females			Ratio of means: Males/females
		N	Range	Mean	N	Range	Mean	
Tetons National Park, Wyo., 9,600′–10,200′	1	9	5–7	5.7	9	4–8	5.6	1.02
Mt. Timpanogos, Utah, 9,000′	2	23	4–7	5.1	17	4–7	5.4	0.94
Wasatch Mountains, Utah	3	15	3–6	4.6	10	3–8	5.3	0.87
Bluebell Knoll, Utah, 9,500′–10,000′ (1)	4	18	0–3	1.2	9	0–3	1.3	0.91
(2)		9	0–3	1.6	8	0–3	1.1	1.48
Cedar Breaks, Utah, 10,500′	5	11	0–5	2.5	22	0–5	2.8	0.89
Circleville Mountain, Utah, 9,700′	6	14	0–4	0.9	18	0–4	2.6	0.35
Snowy Range Pass, Wyoming, 12,500′	7	5	5–7	5.6	3	4–5	4.3	1.29
Long's Peak, Colorado, 11,000′	8	14	2–6	4.4	7	3–6	4.4	1.00
Lefthand Creek, Colorado	9	15	3–7	4.8	15	3–6	4.6	1.04
Leavenworth Valley, Colorado, 10,000′–11,000′	10	4	3–5	4.0	5	2–7	5.0	0.96
Pike's Peak, Colorado	11	4	3–5	4.2	14	3–6	4.6	0.93
vic. Montrose, Colorado, 9,000′–10,000′	12	8	2–6	4.5	4	2–3	2.5	1.80
Wolf Creek Pass, Colorado, 11,500′	13	7	4–5	4.6	9	3–5	4.0	1.14
North Creek, Abajo Mts., Utah, 8,200′	14	16	3–6	4.2	3	3–5	4.0	1.06
Abajo Mountains, Utah, 8,200′	14	10	3–6	4.2	6	2–5	3.3	1.27
Mount Linnaeus, Utah, 10,000′ (1)	14	29	0–6	3.2	31	0–6	3.7	0.86
(2)	14	30	0–7	3.6	27	0–5	3.6	1.00
Abajo Mountains, Utah, 11,000′	14	5	0–4	3.1	12	0–5	3.1	1.00

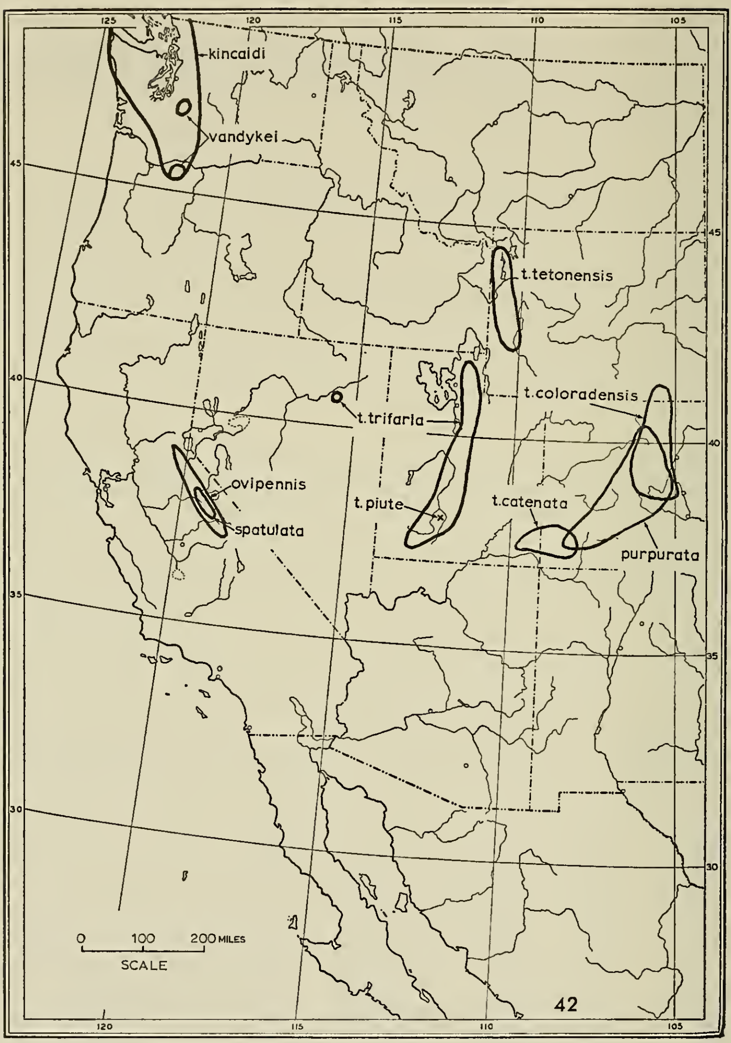

FIG. 42. Distributional area maps of each species of the trifaria and ovipennis groups.

1.80. The females of the latter sample are few, and the abnormally high value may be a result of sampling error. The Circleville sample, however, is large, and this difference is probably of some significance.

In summary, clinal variation seems to be the pattern, with a step-cline between the southwestern Utah samples and the others, and among the former group the Circleville sample is outstanding in its markedly deviant ratio of males/females mean value.

Variation in form and proportions of the apical portion of the male median lobe: Intrapopulation variation in this characteristic is slight but sufficient to prevent its use as a characteristic of specific value. The apical portion is shorter among specimens from western Utah, except for the Circleville Mountain sample. It is longer among specimens of the remaining samples (Figs. 27, 28, 29). The apical portion is arcuate dorsad among males from eastern Utah and western Colorado, but straight among the remaining males. It is narrower among the Colorado specimens, and narrowest among males from western Colorado and eastern Utah.

In summary, the variation pattern seems to be in the form of a four-step morphocline, with one extreme represented by the western Utah samples (excluding the Circleville sample), the other extreme represented by the western Colorado and southeastern Utah samples, and the two intermediate steps represented by Circleville, Wyoming, and northern Colorado samples.

Variation in form of the bursal sclerite: Among the females from northwestern Wyoming, the bursal sclerite is a flattened plate with shallow convolutions. Among the remaining females, this sclerite is pouch-shaped, more convoluted and various in form (Figs. 37, 38, 39, 41).

Summary: Overall, the variation pattern is discordant and consequently complex. The four geographically discrete groups are distinguished more or less clearly from one another, by characteristics of at least one sex. In addition, the southwestern Utah group of samples is the most heterogeneous, and it is reasonable to recognize two groups: one, the Circleville Mountain sample; and two, the remaining samples. Because of their geographical discreteness and slight but constant morphological differences, and in spite of the discordant variation pattern, these groups are ranked as subspecies, and are defined below.

Nebria trifaria trifaria LeConte

Figures 26, 32, 37, 42, 43

Diagnostic characteristics: Elytra dark piceous to black, number of catenations of elytral interval 5 about same for males and females of same population. Median lobe with apical portion short, wide, straight (Fig. 26). Bursal sclerite pouch-shaped, form various (Fig. 37). Length 12.0–13.7 mm. Material dissected: 27 males, nine females.

Geographical distribution: Members of this subspecies are known from the mountain systems of central Utah from Cedar Breaks National Monument in the south, to White Pine Lake near Logan, in the north. Lindroth (1961) and Hatch (1953) reported specimens from Idaho, but we have not seen them. However, we have seen one specimen

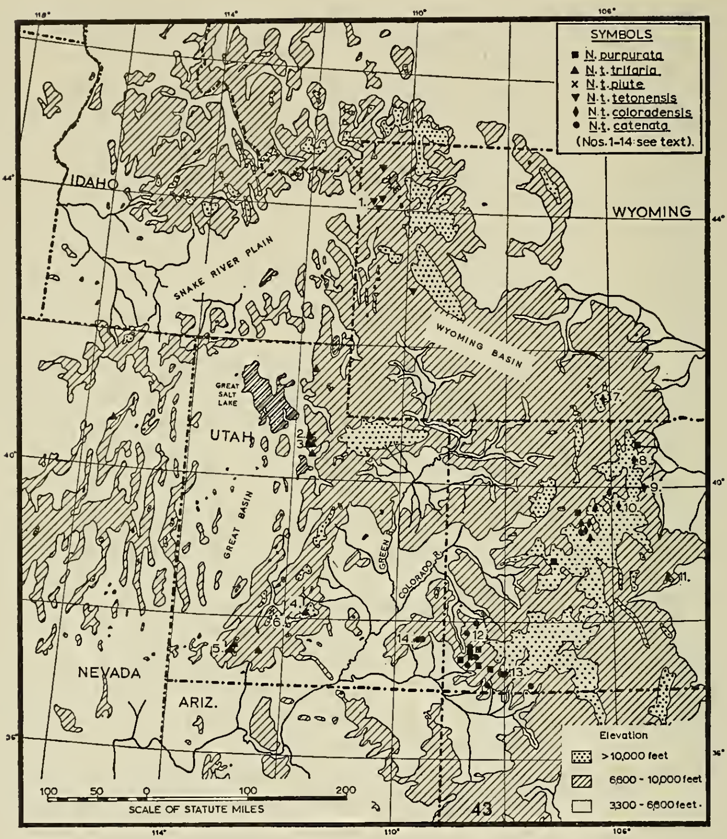

FIG. 43. Distributional area maps (by symbols) of each subspecies of *Nebria trifaria* and of *N. purpurata*, in relation to elevation. Numbers refer to Table 1.

from northeastern Nevada. (See Fig. 42.) We have studied 215 specimens from the following localities.

NEVADA: ELKO COUNTY: Lamoille Canyon, 7,300′ (GRNo). UTAH: CACHE COUNTY: Logan, White Pine Lake, 8,000′ 15 July (CAS). IRON COUNTY: Cedar Breaks, 10,500′, 17 July, 2 August (CAS); Cedar Breaks Nat. Mon., 30 July (ONCO); The Mammoth, top Parowan Mountains, 10,000′, 11–22 July (MCZ). KANE COUNTY: Long Valley Junction, September (CAS). SALT LAKE COUNTY: Alta, 30 June (USNM). UTAH COUNTY: American Fork Canyon, 9,500′, 2–3 August (MCZ); Aspen Grove, Provo Canyon, 20 August (CAS); Glacier Lake, Timpanogos, 9,000′, 7–9 July (MCZ); Mount Timpanogos, 9,000′, 5 July (CAS, USNM); North Fork, Provo Canyon, 9 July, August (CAS, USNM). WAYNE COUNTY: Bluebell Knoll, 22.0 miles south of Teasdale, 9,500′–10,000′, 17 July (DHKa, TLEr). COUNTY UNKNOWN: City Creek Canyon (USNM); Wasatch Mountains, July (CAS).

We suspect that this subspecies will be found in the Uinta Mountains of northeastern Utah, and the Sawtooth Range of southern Idaho.

Nebria trifaria tetonensis new subspecies

Figures 8, 25, 42, 43

Type-locality: South Fork of Cascade Canyon, 10,000′, Teton National Park, Wyoming.

Type-specimens: The holotype male and allotype are in USNM. Both were collected at the type-locality by J. Gordon Edwards and Alice Edwards on 22 July 1960. Thirteen paratypes collected on the same day at the same locality are deposited as follows: CAS—2; DHKa—2; USNM—2; SJSC—5; UASM—2.

Diagnostic characteristics: As in *trifaria* sensu stricto, except apical portion of male median lobe slightly more elongate. Bursal sclerite a flattened plate, with shallow convolutions. Material dissected: seven males, seven females.

Collecting notes: The specimens collected by the Edwards were found at night on snow, actively preying on cold, immobilized insects. One specimen is labeled "carrying live scarab, acc. No. 6269."

Geographical distribution: Members of this subspecies are known from the northwestern mountains of Wyoming from Yellowstone in the north, to Fremont Lake in the south (Figs. 42 and 43). We have seen 23 specimens from the following localities.

WYOMING: PARK COUNTY: Yellowstone, 7,000′–10,000′, 1–19 September (MCZ). SUBLETTE COUNTY: Fremont Lake, 25 July (CAS). TETON COUNTY: Grand Teton Park, July (CAS); head of Leigh Canyon, 9,700′ 11 July (SJSC); South Fork of Cascade Canyon, 10,050–10,200′, 22 July (SJSC); Sunset Lake, Alaska Basin, 9,650′, 29 July (SJSC).

The actual range of this subspecies is probably more extensive than our data show. The outlying mountain peaks in the vicinity of the Tetons are poorly collected, and the higher ones probably harbor populations of this subspecies. In addition, the area between the known ranges of this subspecies and that of *N. trifaria trifaria* is yet to be explored.

Nebria trifaria piute new subspecies

Figures 21, 22, 27, 34, 38, 42, 43

Type-locality: Circleville Mountain, La Baron Lake, 9,700′, 15.9 miles west of Junction, Beaver County, Utah.

Type-specimens: The holotype male and allotype are in USNM. Both were collected at the type-locality on 17 September 1967, Ball, Erwin and Leech. Twenty-eight paratypes, collected on the same day at the same locality, are deposited as follows: CAS—3; DHKa—3; MCZ—3; USNM—3; TLEr—3; UASM—13.

Diagnostic characteristics: As in *trifaria* sensu stricto, except color of elytra violaceous, antennal scape with hind edge slightly more arcuate, catenations of elytra much reduced, especially among males, median lobe with apical portion slightly longer (Fig. 27). Bursal sclerite as in Figure 38. Length 12.8–14.0 mm. Material dissected: six males, three females.

Geographical distribution: Members of this subspecies are known from the type-locality, only. (See Figures 42 and 43.)

Nebria trifaria coloradensis Van Dyke, New Combination

Figures 28, 36, 41, 42, 43

Nebria coloradensis Van Dyke, 1943: 19. Type-locality.—Twin Lakes, Lake County, Colorado. Type-specimen a male!, No. 5298, CAS.

Nebria catenata; Lindroth, 1961: 84 (in part).

Diagnostic characteristics: As in *trifaria* sensu stricto, except apical portion of male median lobe slightly more elongate and slightly more slender (Fig. 28). Bursal sclerite as in Figure 36. Length 12.3–14.0 mm. Material dissected: eight males, four females.

Geographical distribution: Members of this subspecies are known from the Rocky Mountains of southern Wyoming and Colorado, from the Snowy Range of Wyoming to Broadmoor Gold Camp in Colorado. We have seen 128 specimens from the following localities.

COLORADO: BOULDER COUNTY: Long's Peak, 10,000′–11,000′, 2 July (CAS); 5.0 miles east of Ward, Lefthand Creek, 20 July (DHKa). CLEAR CREEK COUNTY: Leavenworth Valley, above Georgetown, 10,000′–11,000′, June (CAS, MCZ, USNM); Silver Plume, 9,000′–10,000′, 15 June (CAS, MCZ); Summit Lake, Mount Evans, 13,000′, 24 July (CAS). EAGLE COUNTY: Redcliff (USNM). EL PASO COUNTY: 9.0 miles east of Broadmoor Gold Camp Road, 2 August (DHKa); Pike's Peak (DHKa). LAKE COUNTY: Leadville, 10,000′–11,000′, 7 July (MCZ, USNM). MESA COUNTY: (USNM). PARK COUNTY: Alma, Mount Bross, 11,500′, 23 July (CAS); Kenosha Pass, 10,000′, 23 July (CAS). SUMMIT COUNTY: 10.0 miles south of Breckenridge, Blue Lakes, 11,400′, 19 July (TLEr). WYOMING: ALBANY COUNTY: Snowy Range Pass, 12,500′, above tree line, June (UASM). CARBON COUNTY: 30.0 miles east of Saratoga, Silver Lake, 10,400′, 22 July (TLEr).

The only area north of the Snowy Range in southeastern Wyoming of an elevation sufficiently high to provide a habitat suitable for the members of this subspecies is Elk Mountain (11,156′) in Carbon County. One of us (TLE) has been on top of that isolated peak during the optimal collecting season, but no specimens of *N. trifaria* were found. Specimens of another as yet undescribed species of *Nebria* were very common, however.

Nebria trifaria catenata Casey, New Combination

Figures 29, 39, 42, 43

Nebria catenata Casey, 1913: 49. Type-locality.—Colorado, as originally given by Casey, but here restricted to the San Juan Mountains of southwestern Colorado. Type-specimen a female!, No. 46849, USNM.
Nebria catenata; Lindroth, 1961: 84 (in part).

Diagnostic characteristics: As in *trifaria* sensu stricto, but apical portion of male median lobe elongate, narrow and arcuate dorsad (Fig. 29). Bursal sclerite pouch-shaped, form various (Fig. 39). Length 12.3–13.7 mm. Specimens dissected: 29 males, eight females.

Geographical distribution: Members of this subspecies are known from the mountain systems of southwestern Colorado south of the Gunnison-Saguache area and in the higher mountains of southeastern Utah (Figs. 42 and 43). We have seen 217 specimens from the following localities.

COLORADO: CONEJOS COUNTY: Valley of Upper San Juan, 7,000′–10,000′, 13–15 August (MCZ). DOLORES COUNTY: Vicinity of Rico, 8,500–10,000 , 19–22 July (MCZ). GUNNISON COUNTY: Canyon of Big Blue, 8,500′, 5–6 July (MCZ). LA PLATA COUNTY: Vicinity of Durango, 5,500–7,000′, 23 July (MCZ). MINERAL COUNTY: Wolf Creek Pass, 11,500′, 17 June (CAS); 2.0 miles west of Wolf Creek Pass, 29 August (DHKa). MONTROSE COUNTY: Vicinity of Montrose, 9,000′–10,000′, 9–10 July (MCZ). OURAY COUNTY: Ouray, 7,500–8,000′, 1–15 July (CAS, USNM); above Ouray, 9,000′–10,000′, July (CAS, USNM). SAN MIGUEL COUNTY: South Fork San Miguel, 8,500′, 14–15 July (MCZ, USNM). COUNTY UNKNOWN: La Plata Mountains, 11,000′–12,000′, 19 July (MCZ). UTAH: SAN JUAN COUNTY: Monticello, 20 July (MCZ). Abajo Mountains, 8,500 and 11,000′, July (UASM), Mount Linnaeus, ca 10,000′, 18 July (DHKa, TLEr), North Creek, 5.0 miles west of Monticello, 8,200′, 18 July (DHKa, TLEr), Spring Creek, 7.0 miles west of Monticello, ca. 8,000′, 18 July (DHKa, TLEr).

According to our maps, there are continuous high mountains along a narrow corridor at the continental divide in Colorado (Saguache County). We have not seen specimens from anywhere near this area, but we suspect that it provides suitable habitats, and furthermore, that this area will be important for gamma-level studies of this subspecies and its sister group, *N. trifaria coloradensis*.

EVOLUTIONARY CONSIDERATIONS

We discuss below the sister-group relationships and zoogeography of the taxa of the *Nebria trifaria* group. The data available at present are not sufficient to extend the discussion to other western species groups of *Nebria*.

Phylogenetic relationships: A phylogenetic classification of the characteristics of the taxa included in the trifaria group is presented in Table 2. Each characteristic is represented by a letter: capital for apomorphic

TABLE 2. Distribution and evolutionary classification of selected character states among the taxa of the *Nebria trifaria* species group

Characteristics	*vandykei*	*purpurata*	*t. tetonensis*	*t. trifaria*	*t. piute*	*t. coloradensis*	*t. catenata*
A. Color of Elytra							
a. black							
A. purple	a	A	a	a	A	a	a
B. Antenna: Scape							
b. cylindrical							
B. swollen	B	b	B	B	B	B	B
C. Pronotum: Sides							
c. narrowly reflexed							
C. broadly reflexed	C	c	C	C	C	C	C
D. Pronotum: Angles							
d. moderately produced							
D. strongly produced	D	d	D	D	D	D	D
E. Elytra: Sides							
e. parallel							
E. rounded	E	e	E	E	E	E	E
F. Hind Wings							
f. apical portion reflexed							
F. apex not reflexed	F	f	f	f	f	f	f

Table 2 (continued)

Characteristics	*vandykei*	*purpurata*	*t. tetonensis*	*t. trifaria*	*t. piute*	*t. coloradensis*	*t. catenata*
G. Male Median Lobe							
g. very short—broad—straight							
G. short—very broad—straight							
G′ short—broad—straight							
G″ longer—broad—straight							
G‴ longest—broad—straight							
G⁗ longest—narrow—arcuate	G	g	G″	G′	G″	G‴	G⁗
H. Female Bursal Sclerite							
h. absent							
H. dome-shaped							
H′ flat; shallow convolutions							
H″ pouch-shaped, convoluted	h	H	H′	H″	H″	H″	H″

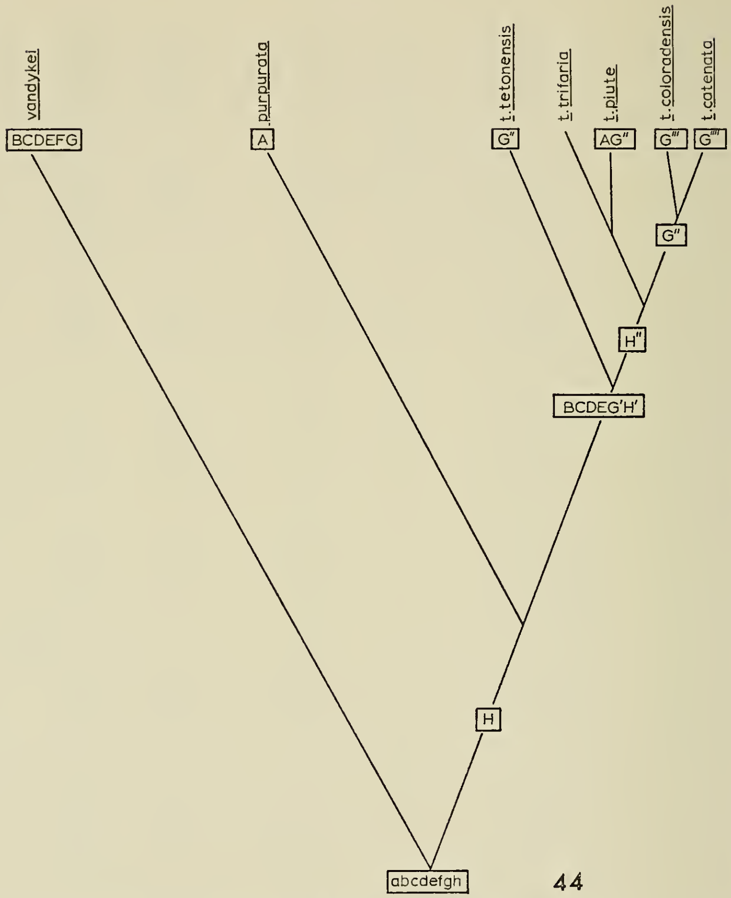

FIG. 44. Hypothetical phylogeny of trifaria group; explanation in text and Table 2.

states, lower case for the plesiomorphic state. These letters are used in the phylogenetic diagram (Fig. 44). The states judged to be plesiomorphic are those which are more widespread in *Nebria* or in other groups of Carabidae than are their respective alternative states; or those which cannot be derived from their respective alternative states in the trifaria group (for example, longer hind wings).

The form of the apical portion of the male median lobe exhibits a number of states which together comprise a morphocline or transformation series. The "very short-broad-straight" condition (Fig. 33) is most widespread among the members of *Nebria*, so it regarded as the most plesiomorphic. The state "short-very broad-straight" (Fig. 23) represents evolution in one direction; and the sequence "short-broad-straight" (Fig. 23), "longer-broad-straight" (Fig. 24), "longest-broad-straight" (Fig. 28) and "longest-narrow-arcuate" (Fig. 29) represents evolution in another direction.

A second morphocline involves the bursal sclerite of the female genitalia. This sclerite is lacking from the bursae of females of *N. vandykei* and females of other species of *Nebria* (for example, those of metallica, paradisi and ovipennis groups). Therefore, this character state is regarded as plesiomorphic. Among females of *N. purpurata*, the bursal sclerite is simple in structure, and in females of *N. trifaria* it is more complex. It is assumed that the *purpurata* condition is more primitive than the *trifaria* condition. Thus the morphocline is: absent; present-simple; present-complex.

A third morphocline involves the number of catenations of elytral interval 5: high, intermediate and low mean values for population samples. It is not clear which of these character states is the more plesiomorphic. Consequently, this characteristic is excluded from the phylogenetic analysis.

The distribution of the character states forms a complex pattern. In external characteristics (form of antennal scape, pronotum and elytra) *N. purpurata* is plesiomorphic, whereas *N. vandykei* and *N. trifaria* exhibit the apomorphic states of these characteristics. In color, *N. purpurata* and *N. t. piute* are apomorphic, whereas the remaining subspecies of *N. trifaria* and *N. vandykei* are plesiomorphic. One plesiomorphic state is shared by *N. purpurata* and *N. trifaria*: size of hind wings. In summary, then, the external characteristics suggest this sequence of taxa: *purpurata-trifaria-vandykei.*

The sequence of the character states of the male median lobe is generally consistent with the external character sequence, except that the evolutionary tendencies in *N. trifaria* and *N. vandykei* are divergent with respect to width.

The sequence of the character states of the female bursal sclerite is incongruous with the sequence of external characteristics. The morphocline is: *vandykei-purpurata-trifaria.*

In summary, the different characters suggest two different systems of relationships. However, there was a single phylogeny, only. The question is, which of the above systems (if either) approximates more closely the true phylogeny? If the sequence indicated by external characteristics is accepted, the loss of the bursal sclerite from *N. vandykei* is required and must be accounted for. If the sequence indicated by the bursal sclerite is accepted, then the apomorphic similarities shared by *N. trifaria* and *N. vandykei* must be accounted for by assuming convergent evolution.

To us, the second alternative seems more likely to be correct. The similarities in external characteristics seem rather simple. They are of the sort which have evolved independently many times among many groups of carabids. On the other hand, it seems unlikely to us that a complex structure, such as the bursal sclerite, would be lost rapidly after having once developed—and this would be required if the first alternative were accepted. Further, the sequence of the median lobe can be rationalized with the bursal sequence if it is assumed that the form of the apical portion of the median lobe of ancestral males of the trifaria group was like that of *N. purpurata*, that this was modified in one direction in the *N. vandykei* line, retained unmodified in the *purpurata-trifaria* ancestral stock, and then modified in a different direction in the *N. trifaria* line. In any event, the male genitalia of *N. purpurata* and *N. trifaria* seem more like one another than either is like the genitalia of *N. vandykei*, and this suggests a relatively more isolated position for the last-named species. These views are summarized in Figure 44.

Zoogeography: The purpose of this section is to interpret the geographical relationships of the extant species of the *N. trifaria* group in terms of present and past climate and topography, in an attempt to explain the present distribution pattern. We accept for purposes of this study that ". . . most contemporary subspecies have differentiated in late Pleistocene time; otherwise, the frequent correspondence seems inexplicable of their ranges with current topographical and ecological features which stem from late Pleistocene events" (Findley and Anderson, 1956). We also accept the assumption that these groups of *Nebria* are cool- or cold-adapted and have been for a long time. This assumption is based on the present distribution, habitat preference, and rearing studies of the Nebriini as a whole; hence cool/cold-adaptedness is judged to be plesiomorphic in Nebriini.

This species group is confined to the mountains of western North America and can be classified in the terminology of Weber (1965) as a sub-element of the cordilleran group of coincident patterns. Actually the distribution of this species group does not coincide exactly with any of the patterns of plant distribution described by Weber, but it is most like his "Central Rocky Mountain-Pacific Northwest sub-element." Probably the ancestor of the *N. trifaria* group evolved in western North America and almost certainly, still earlier ancestors entered the Nearctic Region from Asia, via the Bering land bridge, probably during late Tertiary time. If this is correct, then the *N. trifaria* group can be regarded as a member of the montane Boreal-Asiatic element. Thus, the history of this group is likely to be the same as the history of the vegetational component of this latter element. At present, this is not a very important consideration, for the history of the plants is not well understood. However, it is likely that the history of the vegetational component will be clarified before that of the animal component. As this is achieved, the history of the animal component will be clarified, by analogy.

The species of the trifaria group are represented on tundra (alpine zone) or in coniferous forests of the montane and subalpine zones (for descriptions of these in the eastern Rockies, see Marr (1967) and Blake (1945)). Members of *N. vandykei* and *N. purpurata* are restricted to stream margins, whereas of *N. trifaria* are found both along stream margins and in forests at some distance from open water, or on tundra. The range of each species is discontinuous, and allopatry rather than sympatry is the rule. The most primitive species, *N. vandykei*, is known only from two high peaks in the Cascade Mountains. Five-hundred miles to the east, in the Rocky Mountains of western Wyoming, the northernmost population of *N. trifaria* is encountered, and several hundred miles southeastward in the Southern Rockies (that portion of the Cordillera south of the Wyoming deserts (Weber, 1965)), populations of *N. purpurata* are found (Figs. 42 and 43). The range *of N. purpurata* overlaps that of two subspecies of *N. trifaria*: *t. coloradensis* and *t. catenata.*

The subspecies of *N. trifaria* are more or less widely isolated from each other (Fig. 42). Gaps of 100 to 200 miles separate the nearest known localities for adjacent members of different subspecies (except *t. piute*, which is only 40 or so miles from the nearest populations of *t. trifaria*). Within the range of each subspecies are more or less extensive gaps, some of which are simply the result of lack of sampling. Other gaps are the result of absence of suitable habitats.

Lowland river basins and deserts evidently do not provide suitable habitats for members of the trifaria group, and are barriers to dispersal. The major barriers are the Colorado River and Green River basins; the high desert basins of Wyoming associated with the Green River (Scott, 1965, Fig. 1); the Snake River Plain; the Great Salt Lake desert; the Columbia River basin and associated Palouse country of eastern Washington and Oregon. Kelson (1951) and Findley and Anderson (1956) discuss the importance of some of these barriers to dispersal of boreal or cool-adapted mammals. Barriers of lesser extent are the lower slopes of high peaks within any one mountain system: for instance, within the Wasatch Mountains. Although these areas restrict dispersal of the members of the trifaria group at present, at least some of the barriers were less effective in the past. During the glacial stages of the Pleistocene, the generally cooler and wetter climate plus alpine glaciers, caused a shift downward of several thousand feet of the life zones. Roberts (1970), for example, suggests that the late glacial vegetation at 5,000 feet in southeastern Wyoming was Transition-Canadian Zone open forest. Thus populations of Rocky Mountain species presently confined to the upper slopes, would have been on the lower slopes and in the adjacent valleys during glacial time. The distribution of the populations of *N. trifaria* may have been continuous at the 6,000 or 7,000 foot level, throughout the mountain systems of Wyoming, southern Idaho, northern Nevada, Utah, Colorado and eastern New Mexico.

It is not difficult to imagine that the range of *N. trifaria* was once more extensive than it is at present. It is also apparent that *N. vandykei* had a more extensive range than it has now, but it is surprising that the species seems not to be represented to the east, in the Rocky Mountains of Idaho. Similarily, the species *N. purpurata* seems to be confined to the Southern Rocky Mountains in Colorado, whereas it might be expected to have a distribution pattern more like that of *N. trifaria.* Of course, these species may have been more widespread during full glacial stages, but failed to attain ranges sufficiently extensive to occupy the high country adjacent to their present ranges. Alternatively, they may have occupied adjacent mountain ranges, with the peripheral populations dying out in post-Wisconsin time. For example, post-Pleistocene extinctions of local montane populations of *Marmota flaviventris* Audubon and Bachman were postulated to explain present-day absence of this species from the isolated mountain ranges of New Mexico (Harris, 1970: 24).

The history of dispersal of the *Nebria trifaria* group was probably a series of range expansions during favorable periods followed by range restriction and extinction of local populations during unfavorable times. Probably during periods of range restriction, isolation of populations occurred, and differentiation took place.

The morphological data seem to indicate this sequence of relationships: *vandykei-purpurata-trifaria* (Fig. 44). On the other hand, distributional data suggest a different sequence: *vandykei-trifaria-purpurata.* We interpret the geographical proximity of *N. vandykei* and *N. trifaria* to be secondary. Interpretation of the distribution pattern in terms of the evolutionary one suggests that the ancestral *trifaria-purpurata* population was eliminated from the northern Rockies, but survived in the southern Rockies, followed by pre-Wisconsin dispersal from a southern center, with isolation and subsequent differentiation of the isolates: an ecologically more broadly tolerant *N. trifaria,* and an ecologically more restricted *purpurata.* The area of origin of *N. trifaria* cannot be specified exactly, but it was probably to the west of Colorado.

During the Wisconsin glacial period, *N. trifaria* became widespread and underwent minor, probably clinal, differentiation. In post-Wisconsin time, the range of this species became disrupted. As the climate warmed, the glacial ice melted and the beetles withdrew from lower to higher elevations. Probably the sequence of range interruption was as follows. First, the northern Wyoming populations were cut off as desert conditions developed (or returned) in the lowlands of the southern part of the state. Second, the Utah populations became isolated from the Colorado ones by downcutting of the Green River Canyon (Kelson, 1951). Third, the populations of the Wasatch Mountains became isolated from one another, and since then, *N. t. piute* has differentiated from the other populations. At the same time, the Abajo Mountains populations became isolated from the Colorado ones. Finally, the range of the Colorado populations became divided (as the available data suggest), or the extent of contact was reduced by reduction of favorable habitats. (The high areas between the known ranges of *N. t. coloradensis* and *N. t. catenata* suggest that suitable habitats exist therein, and the gap in distribution is apparent rather than real.)

Except for the most recent part of this evolutionary sequence, the events cannot be accurately timed. It seems reasonable to believe that the present-day distribution of *N. trifaria* is a reflection of Wisconsin and post-glacial events. The slight differences among the geographical isolates suggest a short period of isolation, and the present-day barriers to dispersal were almost certainly not effective during the Wisconsin period. This isolation must be recent, the diagnostic characteristics of the subspecies probably reflecting nothing more than interruption of formerly clinal variation, overlain by slight additional differentiation in isolation. (To support our contention that slight but significant differentiation is likely to be of relatively recent origin, we cite the study of *Mimulus guttatus* DC., by Lindsay and Vickery (1966). They demonstrated that slight geographical differentiation of the Utah populations of this species occurred within the past 4,000 years.) Because of the very narrow geographical range of the subspecies *N. t. piute* and its marked similarity to adjacent populations and absence of indications of clinal variation in its diagnostic characteristics, differentiation almost certainly occurred in post-glacial time, after the isolation of this population from the geographically adjacent ones had taken place. If this were not so, then one would expect to see clinal variation among geographically adjacent populations in the characteristics used to distinguish the subspecies.

It is tempting to suggest that the entire evolution of the extant species of the *N. trifaria* group took place during the latter part of the Pleistocene, with alternating waves of dispersal/range expansion and range contraction/differentiation coinciding with alternating episodes of cooler glacial stages and warmer interglacial ones. However, available fossil evidence for carabids suggests that rate of change requires more time than available during the glacial-interglacial portions of the Pleistocene (see, for example, Matthews, 1968, and Hopkins et al. (1971)). Therefore, the initial dispersal and speciation of the group probably took place prior to the Pleistocene, but the present pattern only became established rather recently, certainly post-Pleistocene.

Conclusion: Although we have used the subspecies category here based solely on distributional and morphological criteria (in the Mayr sense, 1963, 1970) without data from studies in population dynamics, life histories, and genetic capabilities, we feel justified in doing so. Our reasons can be summarized with a statement made by Darlington (1970) at a symposium in Puerto Rico on "Adaptive Aspects of Insular Evolution," "practical revisions . . . allows me to pick out and emphasize special cases which look exciting for future work . . . but they require also, especially, detailed study in the field of the insects' ecology, adaptations, and behavior. My role is to present cases like these as problems for the future."

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